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Abundance signals of amphibians and reptiles indicate strong edge effects in Neotropical fragmented forest landscapes

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Abstract

Fragmentation and habitat loss contribute considerably to global declines of amphibians and reptiles. However, few studies focus on forest edges, created during the fragmentation process, as proximate drivers of the local demographic structure of populations. Here, we use abundance data of amphibians and reptiles to study their responses to forest edges in nine fragmented forested landscapes of the Neotropics. Species-specific abundance data were collected in plots established at varying distances from their respective nearest forest edge. We tested for edge effects on the abundance of species, and used curve clustering techniques to group species with similar edge responses, i.e. species with either increasing or decreasing abundance from the matrix towards the forest interior. We also grouped species that showed no change in abundance with respect to the nearest forest edge and those whose abundance response was unimodal, peaking in either forest habitat or the surrounding matrix habitat. We found that 96% of all amphibians and 90% of all reptiles showed an edge response, with the abundance of 74.5% of amphibians and 57.3% of reptiles decreasing with increasing proximity to forest edges. However, species-specific edge effects were not always consistent, with some species having opposite edge responses when measured in different landscapes. The depth of edge effects exhibited by forest species, i.e. species that increased in abundance in the forest interior, extended up to one kilometre away from forest edges. We show that the median edge effect on forest species extends to 250m within the forest interior, indicating that tropical forest patches with a mean diameter < 500m (minimum area ≈ 78ha) are unsuitable for half of forest-dependent species considered in this study.

Keywords: forest fragmentation, edge influence, species abundance, tropical forest, herpetofauna

1 Introduction

Forest fragmentation acts on top of forest loss, as continuous forest habitats are broken up into increasingly smaller forest patches that are becoming increasingly isolated from each other (Fahrig,

2003). Fragmentation ultimately results in edge-dominated forest fragments, thereby edges or boundary zones differ structurally and functionally from both the original forest and the surrounding non-forest matrix (Saunders, 1991; Murcia, 1995; Cadenasso et al., 1997; Harper et al., 2005). Boundary zones are characterised by abiotic gradients such as wind, temperature or radiation and water fluxes (Didham, 2010), which cause first-order biological changes including altered species composition, distribution and abundance (Holt and Keitt, 2005; Ewers and Didham, 2006a). These biotic effects result in second-order biological changes, such as changes in trophic interactions (Fagan et al., 1999; Holt and Keitt, 2005) and parasitism (Schlaepfer and Gavin, 2001). Both abiotic gradients and biotic changes are examples of ecological phenomena grouped together under the broad concept of "edge effects".

Edge effects can be quantified by their magnitude, i.e. the difference between the lowest and the highest value of a variable measured across a forest edge, and by their extent, i.e. the distance over which the change can be detected (Ewers and Didham, 2006b). Both measures may vary with the quality of the matrix and forest habitat, the latter depending for example on structure and age of the forest patch, shaping the spatially variable patch-matrix contrast (Laurance et al., 2011).

Species respond to the edge differently depending on life history traits, including those linked to habitat specialisation, body size and dispersal capacity (Saunders et al., 1991; Ewers and Didham, 2006a, Stork et al., 2009). Specialisation allows species to adapt to micro-environments as specialized species have a narrower niche breadth, but it can exacerbate the effect of habitat loss (Houlahan and Findlay, 2003; Williams et al., 2008). Indeed, it may render species more vulnerable to habitat changes because forest fragmentation can reduce the probability that the species and its niche are both maintained in the remaining forest fragments (Harris and Silva-Lopez, 1992; Henle et al., 2004). Larger-sized animals are reportedly been more sensitive to fragmentation (Crooks, 2002; Henle et al., 2004; Pineda and Halffter, 2004), although empirical studies report a range of responses (e.g. Suazo-Ortuno et al., 2008; Mendenhall et al., 2014). Dispersal capacity affects the

species ability to travel through suboptimal habitats, less able to provide resources or protection from predators, e.g. low tree cover matrix habitat for forest species (McGarigal and Cushman, 2002).

Biodiversity responses to anthropogenic land use changes are often analysed as species extinctions following habitat loss (Wearn et al., 2012). However, such responses are only the last step of a decline in abundance. Abundance signals in response to land use change, and in particular fragmentation, can be detected earlier, prior to actual species loss, and can be used to identify vulnerable species that are at risk from local extinctions. This information can then be used to design and implement conservation and management actions aimed at reversing local abundance declines. However, modelling the response of abundance-based biodiversity indicators to local drivers (e.g. fragmentation) requires high quality input data (Bellard et al. 2012) and would benefit from a more mechanistic understanding of driver-response relationships at landscape scale.

The abundance and species diversity and richness of mammals and birds typically decrease with increasing fragmentation (Andren, 1994; Laurance et al., 2011), even if some species are disturbance-adapted and can be found in the matrix (e.g. Pardini, 2004). Amphibians and reptiles are considered key indicators of environmental changes (Schlaepfer and Gavin, 2001; Blaustein and Bancroft, 2007), with habitat loss and degradation known to contribute to their observed worldwide declines (Gibbons et al., 2000; Houlahan and Findlay, 2003; Stuart et al., 2004; Cushman, 2006). Yet, comparatively little is known about their responses to fragmentation, especially when edge effects are considered (McGarigal and Cushman, 2002; Gardner et al., 2007a; Carvajal-Cogollo and Urbina-Cardona, 2008, 2015; Suazo-Ortuño et al., 2008). Edges are typically characterised by more open canopies, leading to reduced moisture and increased maximum daily temperatures (Didham and Lawton, 1999; Hardwick et al., 2015). These altered microclimates are particularly likely to affect abundance and distribution of amphibians (Lehtinen et al., 2003), as they respire primary through their moist skin and may thus be more sensitive to desiccation in drier environments. Low dispersal ability of both amphibians (Gibbs, 1998; Demaynadier and Hunter,

1999; Cushman, 2006) and reptiles (Araujo and Pearson, 2005) is likely to further amplify such edge effects.

Lehtinen et al. (2003) used randomisation techniques on species presence-absence data across forest fragments in Madagascar to identify edge responses in amphibians and reptiles, showing that they can display edge and non-edge avoiding strategies. However, their approach could not account for spatial variation in abundance, which may be a more sensitive to fragmentation and hence a more reliable indicator of edge effects on herpetofauna. This is important, as species may show a gradient in their sensitivity to the edge effect, reflecting their varying ability to exploit unique combinations of ecological conditions (Schlaepfer and Gavin, 2002). For example, species declining in abundance from the forest interior to the forest edge may be mislabelled as non-sensitive to fragmentation based on their presence-absence pattern, even though their abundance suggests the likelihood of a local extinction with continuing fragmentation and loss of forest core habitat.

Here, we analyse the abundance responses of 43 amphibian and 61 reptile species to the nearest forest edge in fragmented, human-modified Neotropical landscapes like plantations, primary and secondary forests. We hypothesize that abundance of forest and non-forest species show consistent signals in response to the forest edge, indicating causal impacts of habitat fragmentation, and that we can exploit these signals to monitor the ecological integrity of forests in the landscape. We quantify how far edge effects extend to within forest and matrix habitat by computing the depth of edge influence; and we then use this depth of edge influence to test to what extend habitat suitability decreases for forest species due to fragmentation. Finally, we compare edge responses of species across multiple landscapes to investigate whether edge responses are species-specific or whether they vary among fragmented landscapes, which would indicate that landscape specific characteristics can modify the edge effect.

2 Material and Methods

2.1 Species abundance

We extracted amphibian and reptile datasets obtained at 11 Neotropical landscapes from the BIOFRAG database (Pfeifer et al., 2014) in February 2014, including data from both published and unpublished sources. We subsequently excluded two datasets from our analysis, one of which because of the small number of plots (N = 9) and another one because it was conducted in urban environment. The datasets contain the raw abundance data, i.e. the number of individuals of each species found in each given plot along survey seasons. One dataset solely focussed on measuring abundance of reptiles (Table 1). We concentrated on amphibians and reptiles identified at the level of species (85.7 % of all observations, 249 species retained). We excluded rare species from our analyses, defined as species whose abundance did not exceed three individuals at any plot, as their abundance patterns could not be analysed statistically. Therefore, we retained a total of 104 species (43 amphibian and 61 reptile species) for all subsequent analyses (see Supplementary material 1).

2.2 Study landscapes

The retained datasets originate from sampling in nine fragmented forest landscapes from Central and South America, whose characteristics are summarized in Table 1. The datasets encompass a variety of matrix types, including pasture, secondary regrowth or plantations. The sampling effort varies across datasets, with the number of sampling plots ranging from 15 to more than 150, and the number of known species sampled in these plots from 3 to 40.

2.3 Delineating the forest edge

Location of the forest edge was estimated from high spatial resolution tree cover maps generated from Landsat data between 2000 and 2003 (Hansen et al., 2013; Fig. 1A). We classified the continuous tree cover values as “forest” and “non-forest” using a three-step procedure: (1) homogeneous zones (tree cover variation < 5%) were delineated using morphological segmentation

(marker controlled watershed algorithm, Meyer and Beucher, 1990; Fig. 1B), (2) maps were transformed so that pixels in each homogeneous zones were given the value of the average tree cover in the zone and (3) we computed the value of the tree cover threshold between "forest" and "non-forest" classes so that the intra-class variance of the darkest (high tree cover) and brightest (low tree cover) regions of the image was minimized (Otsu's threshold, Otsu, 1979; Fig. 1C). Tree cover values above threshold were classified as "forest" and tree cover values below threshold as "non forest". The delineation steps prior to thresholding ensure that neighbouring pixels of similar tree cover (differing by less than 5%) are classified within the same category. Therefore, the location of the forest edge, i.e. the interface between "forest" and "non forest" zones, always corresponds to an edge in the landscape.

As the temporal difference between tree-cover map acquisition and species abundance data sampling may introduce an uncertainty in our analysis, we examined whether the studied landscapes had not been significantly altered during this lag period for different studies (see Supplementary Material 2).

2.4 Estimation of edge influence

We used the distance to nearest edge as a proxy measure for edge influence. The distance transform for each forest/non-forest map was computed using the Matlab "bwdist" function implemented from Maurer et al. (2003). The distance transform map contains for each forest pixel its Euclidean distance to the nearest non-forest pixel (as a positive value), and for each non-forest pixel its Euclidean distance to the nearest forest pixel (as a negative value). We then extracted the distance to the nearest edge for each measurement plot from the distance transform map.

2.5 Computing species' response curves to edges

The measured abundance of each species was plotted as a function of distance to the nearest edge (hereafter referred to as "edge response curve"). We searched for shape similarity and natural

grouping within edge response curves using curve clustering. A curve clustering algorithm regroups functions of the same domain (here distance to edge) by shape and location. The implementation we used (Gaffney, 2004) requires a function model to characterise and optimise each cluster. Equation 1 gives the function model we used to cluster edge response curves: a sum of an increasing and a decreasing logistic function. We developed this model to best represent prior knowledge on edge response curves (Ewers and Didham, 2006b): response curves have a sigmoidal shape (species abundance reaches a horizontal asymptote where the edge influence in negligible) and response curves may be monotonic or go through a maximum.

$$\eta = \frac{J}{1 + e^{-B(x-M)}} + \frac{-J}{1 + e^{-B(x-(M+addM))}}$$

Equation 1

Equation 1 is a sum of two sigmoids (logistic functions), modelling the species abundance η as a function of the distance to the nearest forest edge x. The amplitude J is constrained between 0 and maximum abundance, so that the first sigmoid increases and the second sigmoid decreases. B is the steepness of the curve, termed "growth rate" or "de-growth rate" for increasing or decreasing sigmoids respectively. The value of B is positive and is constrained to be below 0.1 to model relatively slow transitions (Ewers and Didham, 2006b). M is the distance to edge for which the growth rate of the first sigmoid is maximum (i.e. M is the location of the inflection point of the sigmoid curve, where the first derivative reaches a maximum and the second derivative goes through zero). We refer to the parameter M as the "growth distance". M is constrained to be within three times the observed distance range: min distance - (max distance - min distance) < M < max distance + (max distance - min distance). M+addM is the inflection point of the second (decreasing) sigmoid, termed "de-growth distance". addM is positive and lower than 3*(max distance – min distance) so that de-growth follows growth and species abundance goes through a

maximum (and never a minimum).

Because the distance to the nearest edge x varies between the minimum and maximum of measured distances, this model (Equation 1 with constrained parameters) can return either an increasing sigmoid (with M+addM >> max distance, Fig. 2 responses 3 and 4), a decreasing sigmoid (M << min distance, Fig. 2 responses 1 and 2), a peaking curve (with M and M + addM within the observed distance range, Fig. 2 responses 5 to 7), or an almost flat curve (M and M+addM outside, Fig. 2 response 0).

2.6 Summarising and comparing edge response curves

We analysed patterns in species edge response curves across datasets by classifying the clusters obtained in the previous step into 8 pre-defined possible response types (Fig. 2). The parameters of the initial clusters were chosen to obtain a set of decreasing, increasing, peaking and flat curves regularly spaced over the range of measured distance. From preliminary testing we estimated that 8 clusters were sufficient to represent the variability of the data. These 8 response types were further re-grouped into three broader categories (Fig. 2) based on the optimised parameters of each cluster (i.e. whether growth and de-growth distances were positive, negative or out of the distance range): species showing no response to the edge (response 0 or "no response", i.e. generalist species), species decreasing in abundance from the matrix to the forest interior (responses 1 and 2 or "non-forest species"), and species increasing in abundance from the matrix to within the forest interior (responses 3, 4 and 5 or "forest species"). The remaining two possible response types (6 and 7) were never observed.

In a second step, we quantified the impact of the edge on the abundance of the species (termed "depth of edge influence") as the location of the minimum of the second derivative of the response curve, or the location of the closest minimum to the edge when there are two minima (Ewers and Didham, 2006b). The location of the minimum of the second derivative corresponds to the distance for which the influence of the edge on the species abundance becomes negligible (cut-

off point). Species present in several datasets were treated as distinct species. This allows us to test whether their edge response curve depends on the landscape in which they are measured.

3 Results

Among the 104 species analysed, six amphibian and 11 reptile species were present in more than one landscape, resulting in a total of 133 observed response curves (51 for amphibians and 82 for reptiles). A significant relationship with distance to the nearest edge was observed for 92.5% of the curves, with only two of the 51 amphibian curves and eight of the 82 reptile curves failing to show any pattern in their abundance responses (Fig. 3).

3.1 Grouping species according to their edge response curves

Response curves of species analysed matched six of eight possible clusters of edge response types (Fig. 2). In total, 85 species showed response curves that resembled those of forest species (38 amphibian and 47 reptile responses), whilst response curves of 38 species (11 amphibian and 27 reptile responses) resembled those of non-forest species. Edge response type 4, i.e. forest species that increase in abundance from the forest edge to forest interior and are absent from the matrix, was the most common edge response (Fig. 3).

The mean depth of edge influence for forest species was + 408m (ranging from -11m to +1900m) and differed significantly from zero (Wilcox test: p-value < 0.001) (Fig. 4). For non-forest species, the mean depth of edge influence was -117m (ranging from -770m to +361m) and also differed significantly from zero (Wilcox test: p-value = 0.014). Estimates of the depth of edge influence for forest and non-forest species were significantly different (Wilcox test: p-value < 0.001). Depth of edge influences did not differ significantly between forest-dependent amphibians and reptiles (mean: 457m and 370m respectively, Wilcox test: p-value = 0.5).

Some non-forest species had a depth of edge influence greater than zero (response type 1, Fig. 2), indicating that these species were also present along forest edges (5 amphibians and 6

reptiles, 45% of non-forest amphibian and 22% of non-forest reptile species). Among forest-species, no amphibian and only two reptiles (6% of forest reptile species) ever occurred in the matrix.

3.2 Same species, multiple landscapes

Seventeen species were present in multiple landscapes. Of which, 11 showed a similar edge response curves across different forested landscapes. These species could therefore be consistently classified as forest or non-forest species (Fig. 5, species for which response types are all in brown shades or blue shades, i.e. 11 last species from *Oophaga pumillio* to *Anolis sericeus*).

However, six species showed different types of abundance response curves to the forest edge in the different landscapes. Two of these species, *Holcosus festivus* (Central American whiptail, a medium-sized ground-dwelling lizard found most commonly in humid and moist lowland forests in Central and South America) and *Thecadactylus rapicauda* (radish-tail gecko, a medium-sized Neotropical gecko with a wide geographic distribution over Central and South America), showed a forest-dependent edge response in one or more landscapes, but had no edge response (i.e. response 0) in another one. Four other species were classified as forest species in some landscapes but as non-forest species in others. *Rhinella marina* (cane toad, also known as the giant Neotropical toad), is a species found in all major IUCN habitat types and listed as invasive in large parts of the world. This species showed three different types of edge response curves in three very different fragmented landscapes (a secondary forest, a cocoa plantation and a *Eucalyptus* plantation). Similarly, *Gonatodes albogularis* showed the same kind of edge response (increasing abundance in the core forest area) in three cocoa plantation landscapes, and a different response (more abundant into the matrix) in a mixed landscape mosaic. Finally, *Anolis lemurinu*s (ghost anole, partly arboreal species of Central and South America) showed four different response types in four landscapes, all of which cocoa plantations. *Sphenomorphus cherriei* showed the same edge response in secondary regrowth and two cocoa plantation landscapes, but another edge response

curve in the third cocoa plantation. For these species, differences among landscape type cannot explain the inconsistency in edge response.

4 Discussion

Our findings provide strong support for the impacts of fragmentation, and in particular of edge effects, on amphibians and reptiles in Neotropical landscapes. By clustering species in their response to forest edges, we can show that over 90% of amphibians and reptile species respond to the forest edge (Fig. 3). We further showed that the abundance of forest species does not increase in forest areas in the immediate vicinity of the edge, but that the response occurs gradually over a spatial gradient that can extend to almost +2000m into the forest (Fig. 4). We suggest that this edge effect is likely to reduce the core area of favourable habitat for forest species, with consequences for estimates of local extinction rates following habitat loss using models based on species-area relationships (Wearn et al., 2012). Even non-forest species were impacted by the presence of forest edges, with 50% of all non-forest species showing an edge effect extending up to 50m into the matrix.

Amphibians are the most threatened group in Red List assessments (Hoffmann et al., 2010). Here, we show that there are clear abundance variations of amphibians and reptiles at local scales, that signal causal impacts of ecosystem degradation through forest fragmentation. This, in combination with dispersal and resource limitations, both typical for amphibians and reptiles, should make them useful indicators to monitor the health of forest ecosystems and to evaluate habitat restoration efforts (Carignan and Villard, 2002). Abundance signals of forest-core dependent species for example, could be used as early warning systems by managers to monitor the ecological integrity of forests at the landscape scale.

A major meta-analysis using 112 published studies concluded that there was “no strong support for the importance of edge effects for either amphibians or reptiles, with a number of studies finding either no effect, a weak effect, or a species-specific effect with no overall change in

311 richness" (Gardner et al., 2007a). Our findings, utilising 104 species in the Neotropics, contradicts
312 this conclusion: the forest edges affect the abundance of both amphibians and reptiles, for both
313 forest and non-forest species. We offer three possible explanations for this apparent contradiction.
314 First, only 48% of the studies reviewed by Gardner et al. (2007a) used species abundances as a
315 parameter for measuring edge effects. Instead, most of their studies focussed on species richness, a
316 metric that does not capture fragmentation impacts on population viability and that fails to account
317 for edge-related turnover in species composition (Banks-Leite et al., 2012). Second, we returned to
318 the raw data from original studies and used exactly the same primary statistics to examine species
319 abundance responses to edge effects, a more sensitive approach compared to relying on reported
320 summary statistics derived using different statistical tests as is typical for meta-analytic reviews.
321 Third, there was a notable difference in localities, with just 27% of the studies analysed by Gardner
322 et al. (2007a) located in tropical landscapes, where our datasets come from. It is plausible that
323 tropical amphibians are inherently more sensitive to forest edges than those in temperate
324 landscapes. This could be linked to tropical species being less thermo-tolerant, as they are more
325 likely to experience less temperature variation (Deutsch et al., 2008). Furthermore, thermal
326 performance curves of ectotherms are typically skewed, dropping sharply as temperature rises
327 above the optimum value. Hence, the vast majority of ectotherms would experience heat stress at
328 temperatures above 40°C, a temperature they are likely to exceed in more sun-exposed
329 environments (Kearney et al., 2009) such as forest edges in the tropics. However, our data do not
330 allow us to test for this mechanistic link and it is possible that the timing of the fragmentation
331 process differs in shaping patterns of edge responses observed at a given time point (Metzger et al.,
332 2009).
333
334 ***4.1 Possible drivers of response curves***
335 Species responses to forest edges were likely driven by changes in habitat structure and associated
336 changes in micro-habitats and micro-climates. We based our analyses on forest fragments

delineated from high spatial resolution tree cover maps, which ultimately can be related to canopy structure and, in particular, canopy openness. Dense canopies filter out up to 95% of the incoming solar radiation (Bonan, 2008), limiting light availability on the forest floor and affecting microclimates within the forest (Ashcroft and Gollan, 2012). Air beneath dense forest canopies is cooler and holds higher relative humidity during the day, and forest microclimate is also less variable within dense forests (Hardwick et al., 2015). The shape of the response curve to the forest edge is likely to also depend on the sensitivity of the species or taxonomic group to this variation in micro-habitats, rendering more specialized species more vulnerable to forest fragmentation (McKinney, 1997; Henle et al., 2004). While habitat generalists may show adaptive switching behaviour in response to variation in habitat availability and quality (Wilson and Yoshimura, 1994), habitat specialists, especially when also characterised by reduced thermo-tolerance and low dispersal capacity, may be less able to cope with the heterogeneous canopies and microclimates characterising forest edges or matrix habitats (Didham and Lawton, 1999).

We found that two thirds of the species present in several landscapes responded in a similar fashion to forest edges in all landscapes (Fig. 5). The remaining species, which displayed different response types in different fragmented landscapes, are all habitat generalists. For instance, the cane toad *Rhinella marin*a is an "extreme generalist" species (IUCN Red List), occurring in almost all habitat types, and the ghost anole *Anolis lemurinus* was described as "extremely variable in all morphological characters as well as in pattern" (Stuart, 1955). We suggest that habitat generalists are more likely to have inconsistent edge responses among landscapes than specialists because they are better able to exploit non-forest habitats within fragmented landscapes (Henle et al., 2004). For example, the cane toad is present in forest fragments, so could conceivably be classified as a forest species in some locations, but is more abundant in matrix habitats such as sugar cane plantations where it would be classified as a non-forest species. In contrast, specialist species may be more sensitive to forest fragmentation because they are unable to cross major gaps between forest patches in the absence of forest corridors (Hobbs, 1992; Henle et al., 2004).

Although, edge effects show complex interactions with other landscape elements and disturbance regimes. For example, Isaacs-Cubides and Urbina-Cardona (2011) found that the anthropogenic disturbance rather than the edge effects affected the presence of some rare anuran species in a Neotropical mountain cloud forest, affecting the habitat quality and population persistence. Moreover, the edge effect may vary with climatic season, some species appearing as edge-avoiders during wet season and edge-loving species during dry season (Schlaepfer and Gavin, 2001).

The heterogeneity in the distribution of different matrix habitat types among some landscapes may also explain the inconsistency of edge responses of a species across several datasets, as matrix habitats may present different levels of suitability (e.g., a secondary forest might be less unsuitable than a pasture for a forest species). Moreover, the high habitat heterogeneity at a finer scale may affect the edge response curves of some species, especially those from amphibians that are sensitive to the proximity of streams or ponds.

4.2 Implications for biodiversity sampling

Our findings suggest that detecting herpetofaunal responses to forest fragmentation requires assessment of abundance trends, collected over a gradient of distances to forest edge that may stretch for at least 250m into the forest interior and 50m into the matrix. Matrix type and context should be taken into account as they could affect species composition and abundance (Santos-Barrera and Urbina-Cardona, 2011). Habitat quality along forest interior could be affected by the intrusion of matrix species that uses canopy openings as stepping stones, altering interspecific interactions into the forest interior (Sartorius et al. 1999, Urbina-Cardona et al. 2006, Carvajal-Cogollo and Urbina-Cardona 2015).

We found that more than 50% of all forest species were affected by forest edges for at least +250m within the forest interior, suggesting that short edge transects may fail to detect important ecological responses. For example, the Turnip-tailed Gecko *Thecadactylus rapicauda* showed no

edge response in the Montserrat landscape, sampled up to 300m within the forest (Young and Ogrodowczyk, 2008), but displayed a clear forest-dependent edge response curve in the Brazilian landscape sampled up to 3780m (Gardner et al., 2007b). However, a rapid assessment of studies on amphibian and reptile edge responses shows that sampling designs rarely include plots farther than a few hundred meters in the forest (e.g. Biek et al., 2002: 75m; Lehtinen et al., 2003: 50m; Reino et al., 2009: 300m; Toral et al., 2002: 250m). This use of relatively short edge transects may have contributed to previous failings to detecting fragmentation impacts on amphibians and reptiles. Ries and Sisk (2010) suggest also that weak research design could lead to "neutral" edge responses (i.e. response type 0).

Similarly, edge transects need to encompass both sides of the habitat edge (Ewers and Didham, 2006a). We found that 50% of non-forest species were affected by the forest edge to at least -50m within the matrix. However, with the exception of one study measuring edge responses (Urbina-Cardona et al., 2012; dataset 1 in Table 1), the sampling design in other studies either ignored the matrix altogether or consistently under-sampled the matrix. For example, Medina-Rangel (2011) compared biodiversity patterns across five habitats (dataset 2, table 1), and hence included some plots in the matrix. However, in the other landscapes, only 12.5% of plots across all studies were placed outside the forest.

We therefore suggest that plots should be sampled from -300m from the edge in the matrix to +1000m from the edge into the forest (if possible given the size of the forest remnants) with particular focus on intense sampling in the zone next to the edge. Information on both matrix and forest structure (their "quality") should be recorded alongside measures of species abundances. Our findings are also relevant for research carried out in fragments that due to their small size may not allow for sampling to be implemented in this design. We suggest that such small forest fragments are likely to be devoid of forest core habitat but rather represent one extended forest edge habitat, determined by biotic and abiotic variables such as wind, weed invasion, tree mortality or phenology (Broadbent et al., 2008). This edge habitat is useful as a stepping stone or habitat

corridor but is unlikely to support forest specialists on the long-term. Studying such small fragments should hence be seen as important for understanding biodiversity response to fragmentation at landscape level, indicating interconnectedness between patches (Ribeiro et al., 2009), but is unlikely to provide mechanistic insight into fragmentation responses of species at patch level.

Here, we analysed the influence of a single forest edge, the one nearest each plot. This represents an important limitation in many fragmentation studies, as it is clear that real landscapes encompass a complex mosaic of forest patches separated by various matrix types. This landscape mosaic configuration could partially explain the high diversity of edge response type of some lizards such as *Anolis lemurinus, Gonatodes albogularis* or *Sphenomorphus cherriei* (Fig. 5). The shape of the response curve is also likely to be affected by landscape-scale fragmentation characteristics including matrix contrast, patch connectivity and the presence of multiple edges (Ries et al., 2004; Fletcher, 2005). For example, the Mexican landscape in our study consists of forest fragments separated by pasture, facilitating a clear delineation of fragments based on strong contrasts in tree cover. The matrix in the Colombian landscape, on the other hand, includes various non-forest habitat types with a gradient of tree cover contrasts, complicating the delineation of fragments juxtaposed to the surrounding matrix. Modelling abundance changes of species in response to fragmentation based on species' perception of the continuous variation in tree cover across the landscapes would be an interesting direction for future studies.

Furthermore, efforts in the field should include measures of biophysical structure, and in particular canopy structure. Rapid canopy structure assessments such as those based on hemispherical photography are increasingly implemented following standardised sampling designs. They allow for rapid and cost-effective retrieval canopy lead area index and fraction of absorbed photosynthetically active radiation (Pfeifer et al., 2012, 2014), which mechanistically link to microclimates (Hardwick et al., 2015). These field estimates can then be up-scaled to landscape structure maps using increasingly available high spatial-resolution satellite data (Pfeifer et al.,

2016), which can be utilised for detailed analyses and interpretation of biodiversity changes induced by fragmentation. Future analyses could use vegetation productivity or tree cover maps created directly from Landsat images acquired as close as possible to the sampling date in the field. Future campaigns sampling biodiversity in fragmented forested landscapes could make use of recent developments in remote sensing and ecological sciences, acquiring measures of canopy cover following standardised sampling designs in the field and using remotely sensed data to up-scale those measures to landscape maps (Pfeifer et al., 2016).

4.3 Conservation implications

In this study, the depth of edge influence was ≥ 250m for at least 50% of the species (Fig. 4). Thus, the edge zone extends on average from 0 to 250m within the forest habitat, so that a round forest patch with a mean diameter < 500m would contain no viable core area for the forest species. This has strong consequences in terms of conservation, as it clearly shows that large forest patches must be conserved to protect forest species. Otherwise, only species able to use the immediate vicinity of forest edges (i.e. less prone to edge effect) are likely to survive. This is of a particular concern under current road expansion efforts (Laurance et al., 2014), which increasingly cut into fragments the remaining wilderness areas. In the Brazilian Atlantic forest for example, more than 80% of the fragments are < 50ha and half of the remaining forest is closer than 100m from an edge (Ribeiro et al., 2009), whereas up to 50% of the dry tropical forest in Central and South America remain as fragments < 10km² (Portillo-Quintero and Sanchez-Azofeifa, 2010). In our study, the range of depth of edge influence from 200m to 300m into the forest includes almost 60% of the forest species, with 85% of forest species showing a depth of edge influence greater than 200m.

Our approach of computing species response curves to the nearest forest edge explicitly quantifies the depth of edge effect, which ultimately is a measure that can be used to delineate the minimum forest area required to protect forest-dependent and edge-sensitive species in any given landscape. This measure can also be used in ecological networks, i.e. large-scale corridors that

connect habitat patches for animal dispersal (Samways et al., 2010): these networks create new edges and it is relevant to know the depth of edge effect on the targeted species in order to design them (Pryke and Samways, 2012). For example, Dixo and Metzger (2009) showed that too narrow corridors may prevent leaf-litter lizards from recolonizing forest fragments.

Furthermore, our approach can be used to assess responses of species within a taxonomic group measured in the same landscape. It allows quantifying the forest area needed to maintain the majority of species. This measure can then be used to identify and delineate those areas in land cover maps that meet (or could potentially meet under restoration efforts) the criterion of maximum patch size, and therefore the minimum critical forest area required to maintain forest biodiversity over time. This method is thus particularly relevant in prioritizing landscapes for conservation when several species are involved (Moilanen et al., 2005). Here, 80% of all forest species showed a depth of edge influence narrower than 450m, indicating that a forest patch with a diameter of approximatively 1km (~ 80ha area) provides a suitable core area of at least 3ha (100m diameter) for most edge-affected species.

More recently, various indicators have been developed to assess the population abundance dimension of biodiversity, including the Living Planet Index (LPI), the Wild Bird Index (WBI) and the European Butterfly Indicator for Grassland Species (Pereira et al., 2012). Here we show that abundance adds significant information, allowing to develop a more mechanistic understanding of how species respond to land use change and in particular deforestation. This understanding, in turn, will improve our capacity to predict biodiversity change following habitat loss and fragmentation, paving the way for managing biodiversity change in human-modified landscapes. Many studies aiming to predict biodiversity loss following habitat loss and fragmentation continue to link species distributional data to models of species-area relationships. Matthews et al. (2014) showed that focussing on total species richness instead of separating specialists and generalists may underestimate the loss of specialists following fragmentation, whilst overestimating the value of smaller fragments. Here, we go one step further showing that the sensitivity of specialists varies

and that abundance signals in response to forest edge can be used to delineate the forest habitat that remains useful for forest specialists. Future studies should include comparisons between both approaches, using species richness and abundance measures, to identify under which situations species richness would be insufficient to plan for management of biodiversity loss at landscape scale.

5 Conclusion

Here, we present for the first time strong support for pervasive forest fragmentation impacts on a vast number of amphibian and reptile species in Neotropical forest landscapes. The extent of this edge effect stretches farther than detected by most studies, both within and outside forest remnants, necessitating a rethink of how we sample biodiversity in fragmented landscapes. The edge responses of amphibians and reptiles are likely to depend at least in part on their life-history traits, such as body size and degree of habitat specialization, although this will require considerable further work to demonstrate general patterns of trait-determined edge sensitivity. This may be a promising avenue for future work, however, as it could allow us to identify the species most at risk from future land use changes involving deforestation and forest fragmentation, and ultimately design landscapes that can maximise biodiversity and functional diversity values under land use changes.

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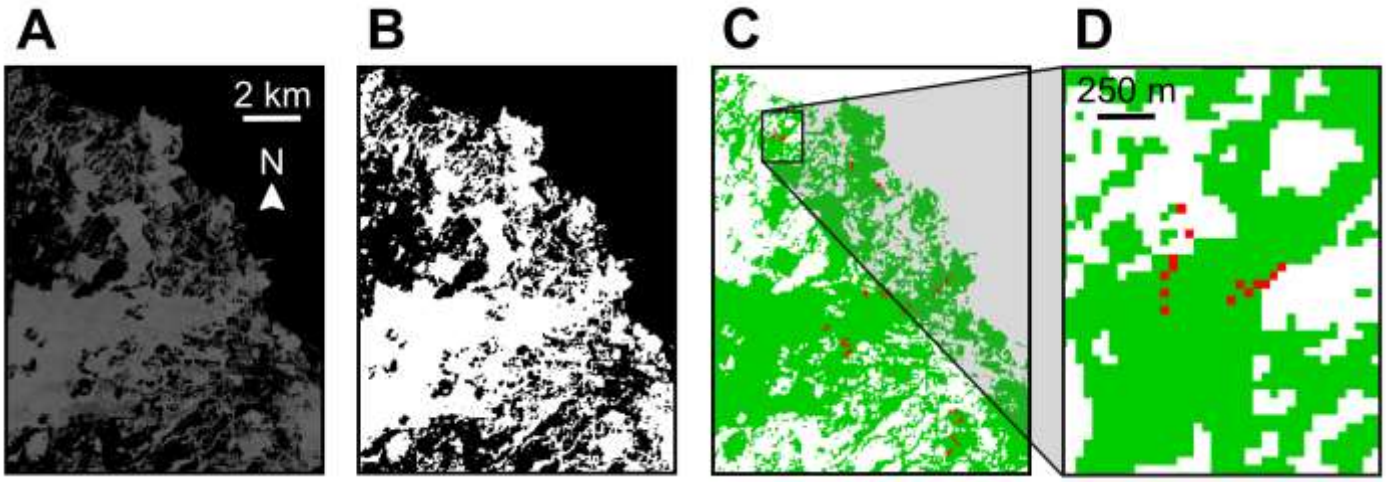


752 **Figure 1: Forest fragments delineation and distance to edge computation**

753 The different steps are shown for the dataset #1 in Mexico (cf. Table 1). A: grey scale tree-cover
754 map from Landsat data (light: high tree cover, dark: low tree cover); B: binary map obtained with a
755 tree-cover threshold of 41% (forest in white, non-forest in black); C: binary map with plot locations
756 in red (green: forest, white: non-forest), D: zoom of C to show the distribution of plots across the
757 forest edge.

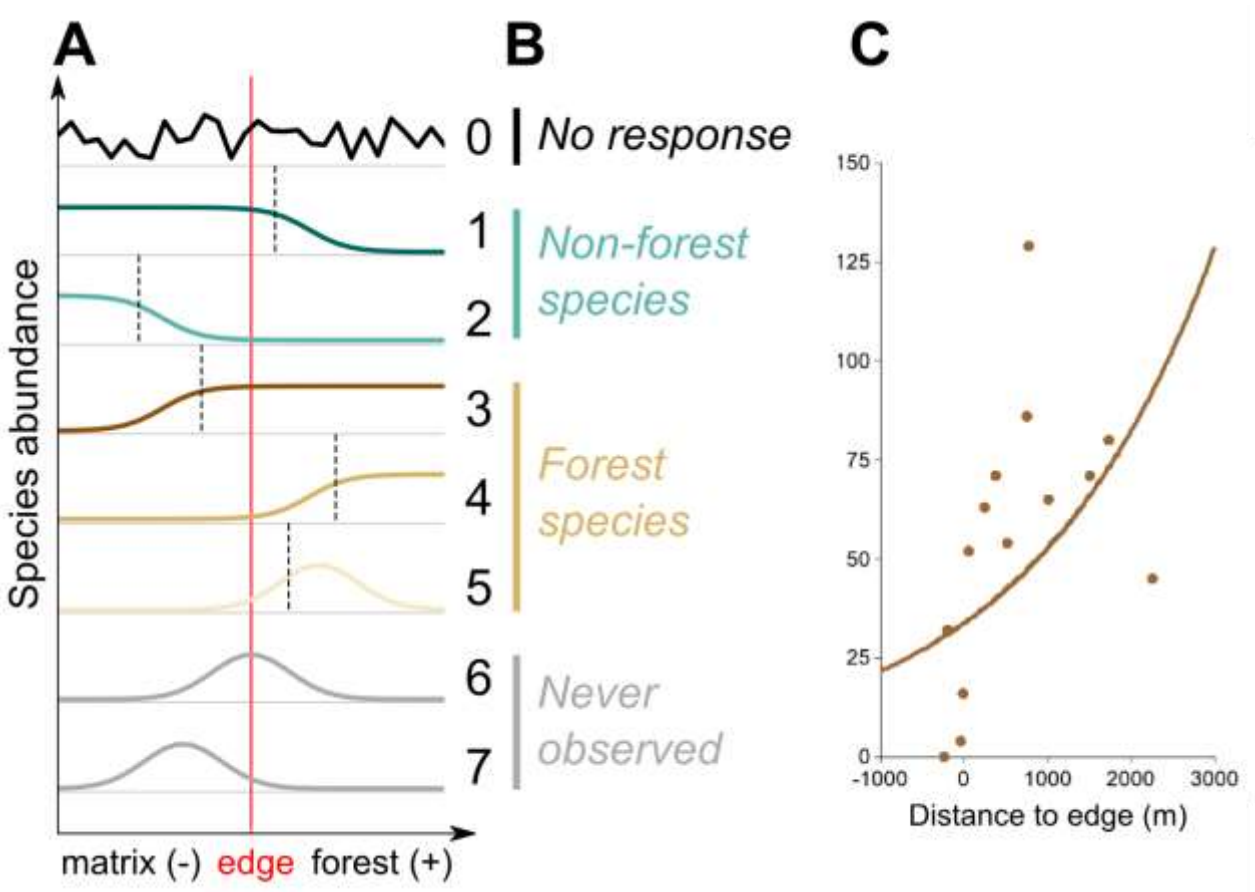
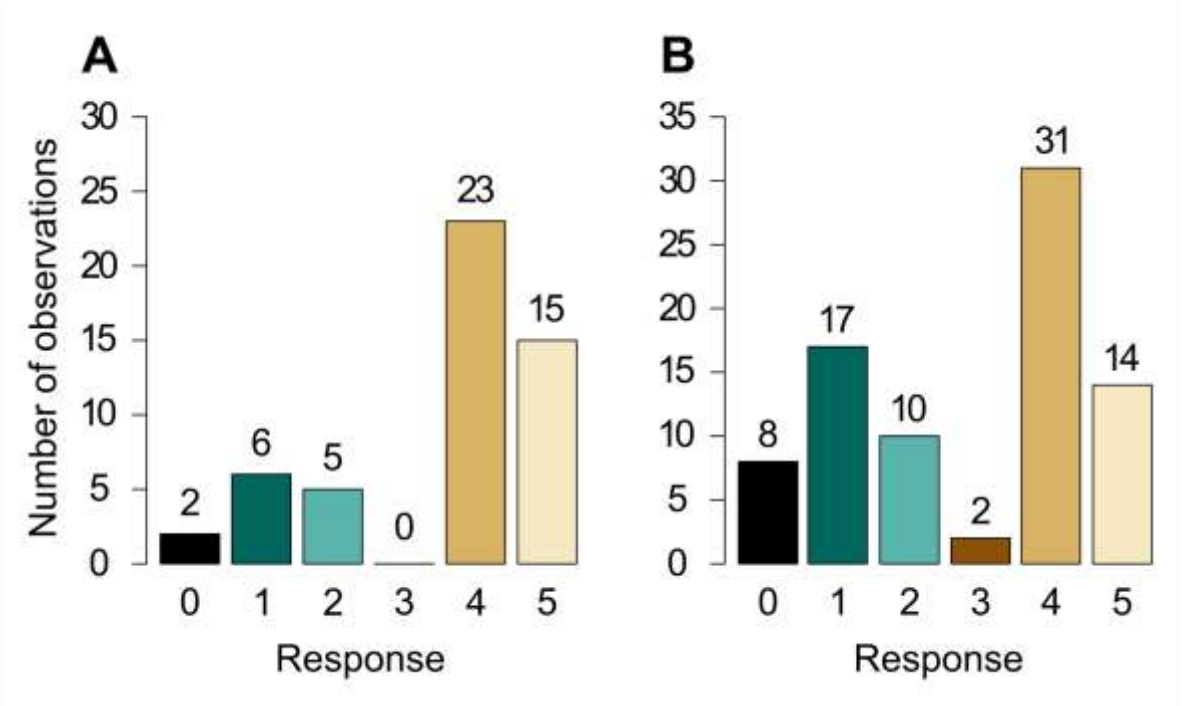


Figure 2: Different types of edge response (A) and species categories (B)

There are height different edge responses, from 0 to 7 (A). Species abundance is directly plotted with respect to distance to edge. Red line corresponds to the physical edge of the forest; the forest is on the right of the edge (positive values of distance to edge), the matrix on the left (negative values) ; the depth of edge effect is shown in dotted line. Species are grouped into categories (B) regarding to their edge response: 'no response' when edge response is 0 (no clear pattern of change in abundance across the edge), 'non-forest species' when edge response is 1 or 2 (decreasing abundance from matrix to forest interior), 'forest species' when edge response is 3, 4 or 5 (increase in abundance from matrix to forest interior). Edge responses 6 or 7 were never observed. Panel (C) shows an example of abundance data from dataset #9.

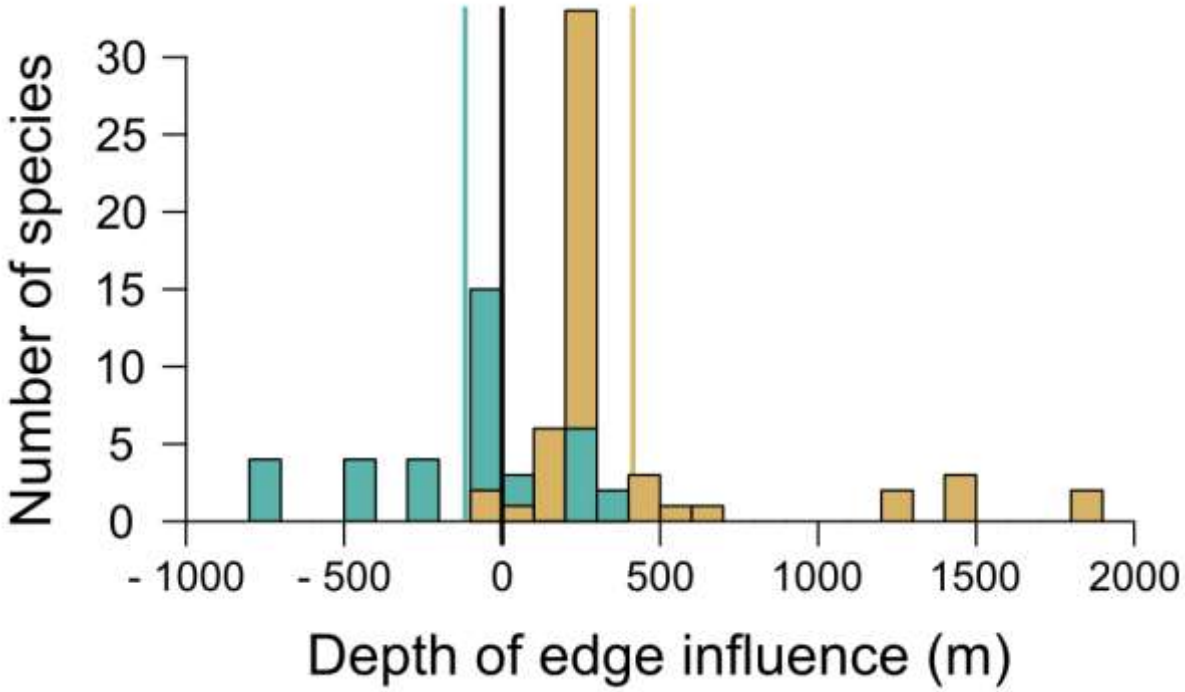


769

770 **Figure 3: Number of recorded edge responses of each type for (A) amphibians and (B)**

771 **reptiles.**

772 Exact numbers of species per edge response type are shown above.

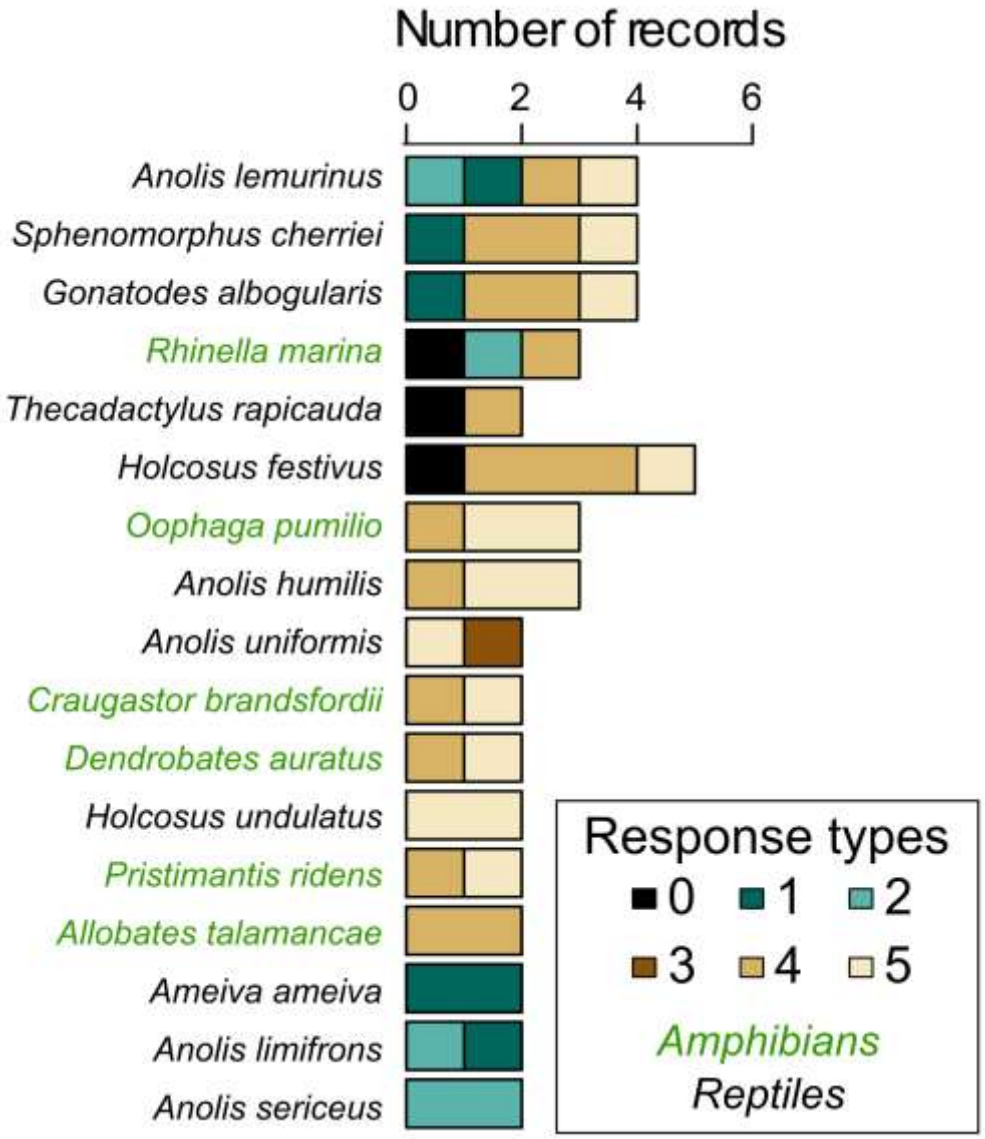


773 **Figure 4: Distribution of the depth of edge influence for forest (brown) and non-forest (blue)**

774 **species**

775 Brown line represents the mean depth of edge influence for forest species (+408m), blue line for

776 non-forest species (-117m) and black line the edge.



777

778 **Figure 5: Edge responses of the 17 species present in several datasets.**

779 Response types indicating a forest-dependence of the species are coloured in shades of brown.

780 Response types indicative of forest independence are coloured in shades of blue. Amphibians

781 names are indicated in green, reptiles names in black.

782 **Table 1: The nine datasets used for analyses**

783 Summary of the datasets characteristics and the mean depths of edge influence on forest-dependent and forest-independent species. [1]Number of

784 individuals of abundant species in brackets, [2]number of abundant species in brackets, [3]number of species in brackets.

Data set	Location	Number of plots	Nb. of individuals of known species[1]	Known amphibian species[2]	Known reptile species[2]	Mean depth of edge influence on forest species (m)[3]	Mean depth of edge influence on non forest species (m)[3]	Matrix characteristics	Date of sampling	Publication
1	Mexico	162	4332 (4098)	22 (14)	40 (9)	+ 108 (4)	+ 89 (8)	Secondary regrowth or pasture.	2003-2004	Urbina-Cardona et al. 2006, 2012
2	Montserrat	30	3174 (3153)	3 (1)	4 (2)	--	- 85 (2)		2005-2006	Young and Ogrodowczyk 2008
3	Colombia	40	795 (713)	0	40 (18)	- 11 (2)	- 163 (10)	Tree-lined savannahs, palm-grove, riparian, dry or chasmophyte forest.	2006-2007	Medina-Rangel 2011
4	Costa Rica	39	725 (658)	19 (6)	23 (8)	+ 441 (7)	- 770 (2)	Cocoa plantations	2009-2010	Data provided by Eduardo Somarriba
5	Guatemala	39	165 (108)	10 (2)	6 (4)	--	--			
6	Panama	43	1251 (1142)	29 (10)	24 (7)	+ 508 (11)	- 244 (4)			
7	Honduras	40	328 (263)	11 (1)	26 (7)	+ 682 (1)	- 247 (6)			
8	Nicaragua	40	458 (422)	12 (6)	18 (7)	+ 167 (3)	- 30 (2)			
9	Brazil	15	2336 (2296)	18 (11)	30 (20)	+ 288 (19)	+ 11 (3)	Primary, secondary and *Eucalyptus* plantation forests	2004-2005	Gardner et al. 2007b